J. VAN TOL

National Museum of Natural History, Leiden, The Netherlands

THE ODONATA OF SULAWESI AND ADJACENT ISLANDS

Part 3. The genus *Macromia* Rambur (Corduliidae)[1]

Tol, J. van, 1994. The Odonata of Sulawesi and adjacent islands. Part 3. The genus *Macromia* Rambur (Corduliidae). – Tijdschrift voor Entomologie 137: 87-94, figs. 1-25, table 1 [ISSN 0040-7496]. Published 15 July 1994.

The *Macromia* species of Sulawesi (Celebes) are detailed, and a key to the species is provided. One new species, *Macromia celebica* sp. n., and the hitherto unknown female of *M. irina* Lieftinck are described. The occurrence on Sulawesi of *M. moorei fumata* Krüger is considered doubtful. The phylogenetic relationships of the Indo-Australian species of *Macromia* are analysed. The Sulawesi species are shown to have a sister group relationship to the monophyletic group of the Papuan species. *M. chalciope* from Halmahera is considered the most recently evolved taxon. These results are compared with recent reconstructions of the geological history of the region.

J. van Tol, National Museum of Natural History, P. O. Box 9517, 2300 RA Leiden, The Netherlands.

Key words. – Odonata; Corduliidae; *Macromia*; new species; phylogeny; biogeography; Indonesia; Sulawesi; New Guinea.

Hitherto, only two species of the rheophilic dragonfly genus *Macromia* Rambur have been mentioned from Sulawesi (Celebes), viz. *M. moorei fumata* Krüger and *M. irina* Lieftinck (Lieftinck 1950: 714-716). Specimens of *Macromia* that were recently collected in the southern part of Central Sulawesi, appear to belong to a species as yet undescribed. The number of species reliably recorded from this island, however, remains two, since the only record of *Macromia moorei fumata* must be regarded doubtful (see below).

The dragonflies of the virtually cosmopolitan genus *Macromia* are remarkable insects in many respects. With more than 120 species, several of which polytypic, *Macromia* is one of the largest genera of the Anisoptera. They are especially speciose in the tropical areas of the Old World. In Europe (one species), North America (nine species) and Australia (two species), they are far less numerous. All other species are confined to Africa and Southeast Asia.

Our present knowledge of the *Macromia* species of Southeast Asia is mainly based on the studies of Krüger (1899) and especially Lieftinck (1929, 1950, 1971a; see also 1954).

Due to their elusive behaviour, most species are poorly represented in collections. In fact, many are only known from the type series, often consisting of one specimen only. Most species are fierce flyers. The larvae seem to be quite stenotopic, so that larvae as well as adults can only be found in very restricted parts of streams. Notwithstanding their strong flying capabilities, many species have small ranges, apparently due to the fact that they seldom fly far from their breeding sites.

In the present paper I describe the new species from Sulawesi, provide some new observations on *M. irina*, and give a key to species recorded from Sulawesi. Finally, after having analysed the affinities of the Sulawesi species to those of the Oriental and the Papuan regions, I propose a hypothesis for a scenario of the biogeographical history of this genus in the Indo-Australian region.

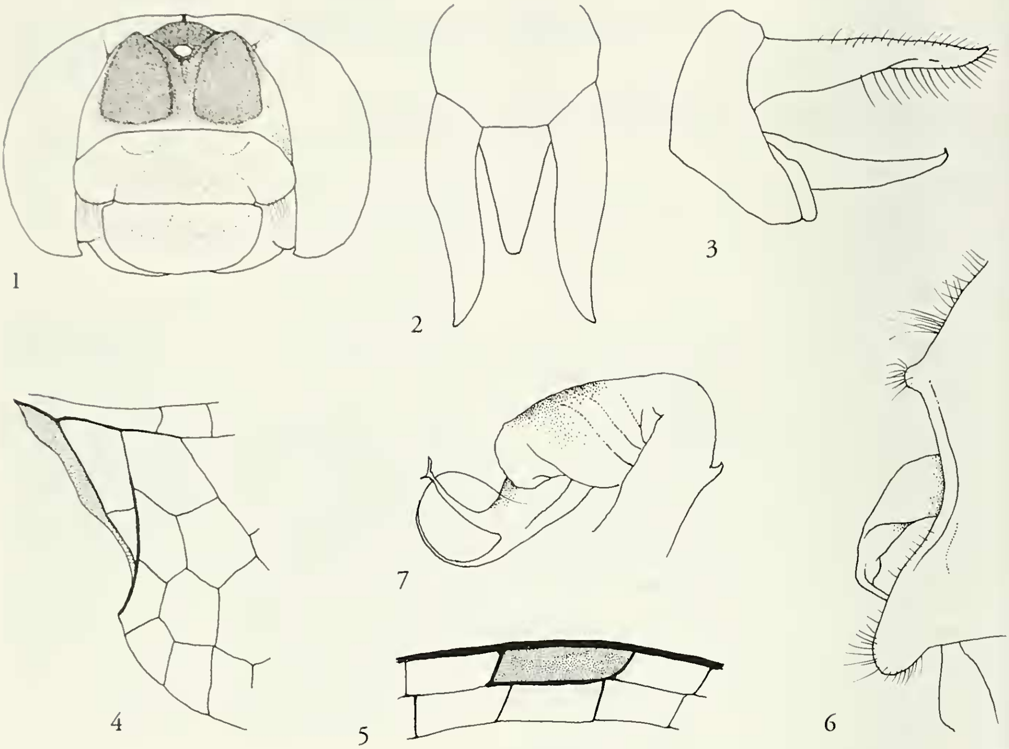
SYSTEMATIC PART

Key to the *Macromia* species of Sulawesi

1. Outer margin of superior appendage of male with well-developed tooth-like tubercle approximately halfway (cf. fig. 18); vertex bilobed (cf. figs. 22, 23); thorax green with metallic lustre .... *M. moorei fumata* [Occurrence on Sulawesi doubtful].
– Outer margin of superior appendage of male

---

[1] Part 2: Zoologische Mededelingen [1987] 61 (13): 160-176.



Figs. 1-7. *Macromia celebica* sp. n. – 1, Head in frontal view; 2, Anal appendages of male, dorsal view; 3, Idem, left lateral view; 4, Base of right hind wing, male; 5, Pterostigma of right fore wing; 6, Accessory genitalia of male, left lateral view; 7, Fourth segment of penis, left lateral view.

somewhat curved inwards, in some specimens with very small teeth along the margin, but especially in dorsal view not a conspicuous extero-lateral tooth (figs. 2, 9); vertex dorsally smoothly rounded, without a paired tubercle (figs. 1, 8); thorax green or brown 2

2. Appendix inferior distinctly shorter than superiors (figs. 2, 3); coloration at least on synthorax green with greenish blue metallic shine; frontal side of head brownish black .... *M. celebica* sp. n.

– Appendix inferior approximately as long as superiors (figs. 9, 10); coloration without any indication of metallic lustre, but body generally orange-brown; head orange-brown with some middle-brown parts, but without conspicuous brownish black frons .... *M. irina*

Macromia celebica sp. n.
(figs. 1-7)

Type material. – Holotype ♂. Indonesia. Southern Central Sulawesi. Puncak Palopo. 600-1000 m. October 1993. Leg. Yohan R. (JvT 6007) (MBBJ). – Paratypes: 2♂, same data (JvT 5930-5931) (RMNH).

Description. – A medium-sized *Macromia*, with green thorax and dark abdomen.

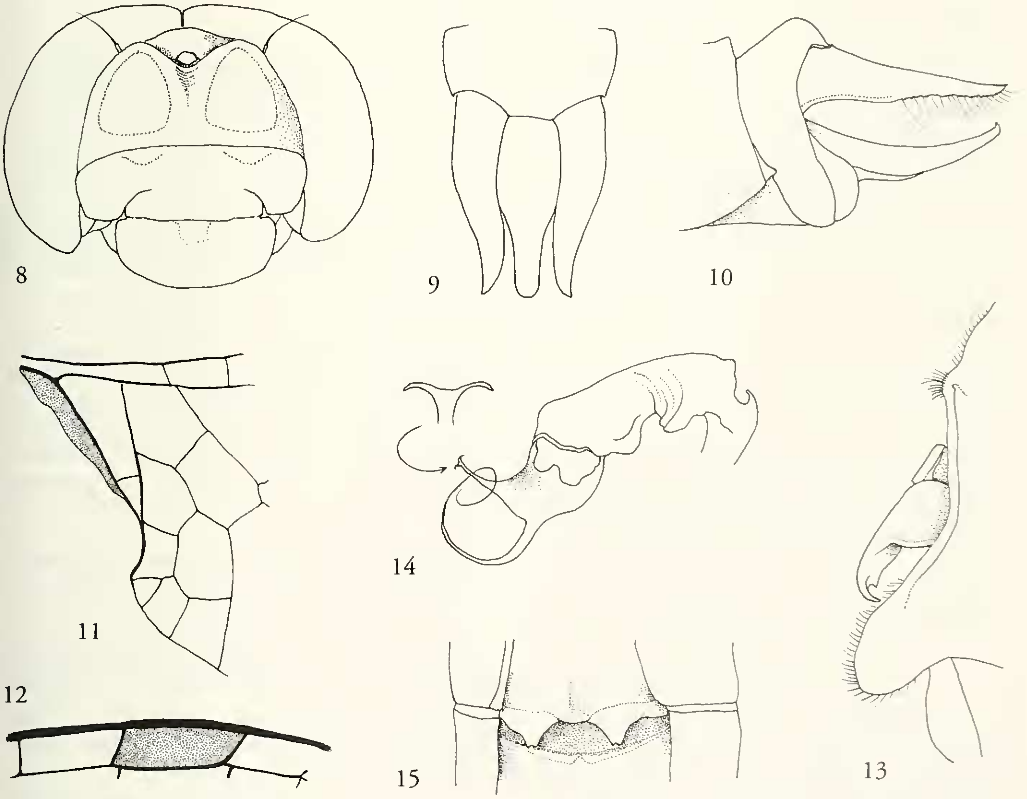
Male. Head with labium, labrum and clypeus orange-brown, especially clypeus without yellow markings, labrum with outer corners darker. Pyramidal processes of frons high and subacute (fig. 1); frontal side very flat, more or less triangular, with very fine transverse striae from upper-inner to lower-outer corner of each side; frontal and upper parts of frons shiny black with blue metallic lustre; frons against eyes orange-brown as lower part of face; vertex black with fine punctation, the paired dorsal tubercles hardly discernable, the lateral angles tapering into small projecting cones on top of which the lateral ocelli are situated (shape as in *irina*; *westwoodii* has somewhat more pronounced dorsal tubercles), covered with thin setae. Occiput shiny black with very fine punctation. Antennae brownish black.

Thorax. Brilliant metallic green, densely covered with long and slender creamish white setae; antehumeral stripe yellow and distinct, somewhat tapering dorsally, extending dorsally to ca. three-seventh of mesepisternum, ventrally continuing over mesinfraepisternum; yellow stripe over spiracle rather narrow, tapering in width dorsally and nearly reaching the upper margin of episternum. Pale stripe on lateroventral part of metepimeron covering anterior anterior half (stripe absent in *chalciope*). Legs long and slender, hind femur 10 mm, reaching to base of posterior hamulus, colour brown, keel on fore leg very short, ca. 1 mm, not reaching the apex, middle tibia without keel, hind tibia with long keel from ca. 2 mm from base of tibia to less than 1 mm from its apex.

Wings relatively short, fore wing with 17-18 Ax, 8 Px; hind wing with 11 Ax, 11-13 Px; fore wing with 7 Cux, hind wing with 5 Cux (incl. subtriangle); anal loop 7-9 cells without central cell; anal triangle relatively short (fig. 4; cf. *M. chalciope*, fig. 19); discoidal triangle of hind wing very narrow; pterostigma (fig. 5) reddish brown, anterior side ca. 2.0 mm.

Abdomen brownish black with some blue-green metallic lustre especially on first few segments; yellow spot on anterior side of segment 7; general shape anteriorly slender, especially segment 7-9 significantly widened; tergites ventro-anteriorly somewhat paler, dark or middle-brown. Spot on segment 7 consisting of a complete ring covering anterior one-fourth of segment, medio-dorsally extending posteriorly for another one-eighth segment length and ca. one-third the segment's width. Segment 10 rather short, mid-dorsal process not spine-like, but consisting of a low triangular-shaped subterminal tubercle. Appendages (figs. 2-3) with superiors in dorsal view rather slender, significantly longer than inferior, basal two-fifths rather straight, then innerside slightly tapering posteriorly and outerside strongly tapering, caudalmost part somewhat curved outwards; no trace of a lateral tubercle on superior appendage.

Secondary genitalia: anterior side margin of tergite 2 with dense setae, a mixture of strong and soft setae, longer than in *irina*; also tuft of setae on ventral tu-



Figs. 8-15. *Macromia irina* Lieftinck. – 8, Head in frontal view; 9, Anal appendages of male, dorsal view; 10, Idem, left lateral view; 11, Base of right hind wing, male; 12, Pterostigma of right fore wing; 13, Accessory genitalia of male, left lateral view; 14, Fourth segment of penis, left lateral view; 15, Valvula vulvae, female.

bercle of tergite longer; genital lobe directed posteriorly, elongate, and tapering towards the top, but tip not acute; posterior hamulus glossy brown, basally coloured brown, the straight outer part pale brown, and the endhook reddish brown, curved strongly (90°) inwards, endhooks in ventral view slightly diverging, the tip reaching ca. two-thirds of genital lobe.

Measurements. – Abdomen, incl. appendages 48 (paratypes 46-48) mm, hind wing 42 (paratypes 42-43) mm

Female. – Unknown.

Differential diagnosis. – Differs clearly from the only other Sulawesi *Macromia* by the presence of green metallic lustre, the black markings on the frons, the presence of an antehumeral stripe; structurally the short inferior appendage, and shape of abdominal segment 10 are diagnostic. Both Sulawesi species can be distinguished from other Indo-Australian *Macromia* by the intermediate sized pterostigma, the very narrow discoidal triangle of the hind wing, and especially the rounded (not bilobed) vertex. Also, the superior appendages lack an extero-lateral tooth, but are not particularly slender. The Papuan *Macromia* have extremely slender superiors with or without an extero-lateral tooth (fig. 20), while the Oriental species have rather solid appendages with a more or less conspicuous extero-lateral tooth (fig. 18).

Remarks. – Although this species differs in many respects from *M. irina*, I consider it the sister species of *M. irina*. This view is based on shared, presumably apomorphous, character states in the structure of vertex and superior appendage of male (see below).

Distribution. – Only the southwestern part of Central Sulawesi. Collected between 600-900 m.

Macromia irina Lieftinck
(figs. 8-15)

Macromia irina Lieftinck, 1950: 714-716. Holotype male 'S Celebes, foot of Mt Lompobatang, Borong Rapao, 800 m, 12.viii. 1949, leg. A. Diakonoff' in RMNH [examined]. – Lieftinck 1971b: 94 [note on type]; Askew et al. 1989: 118 [records Northern Sulawesi, Dumoga Bone National Park].

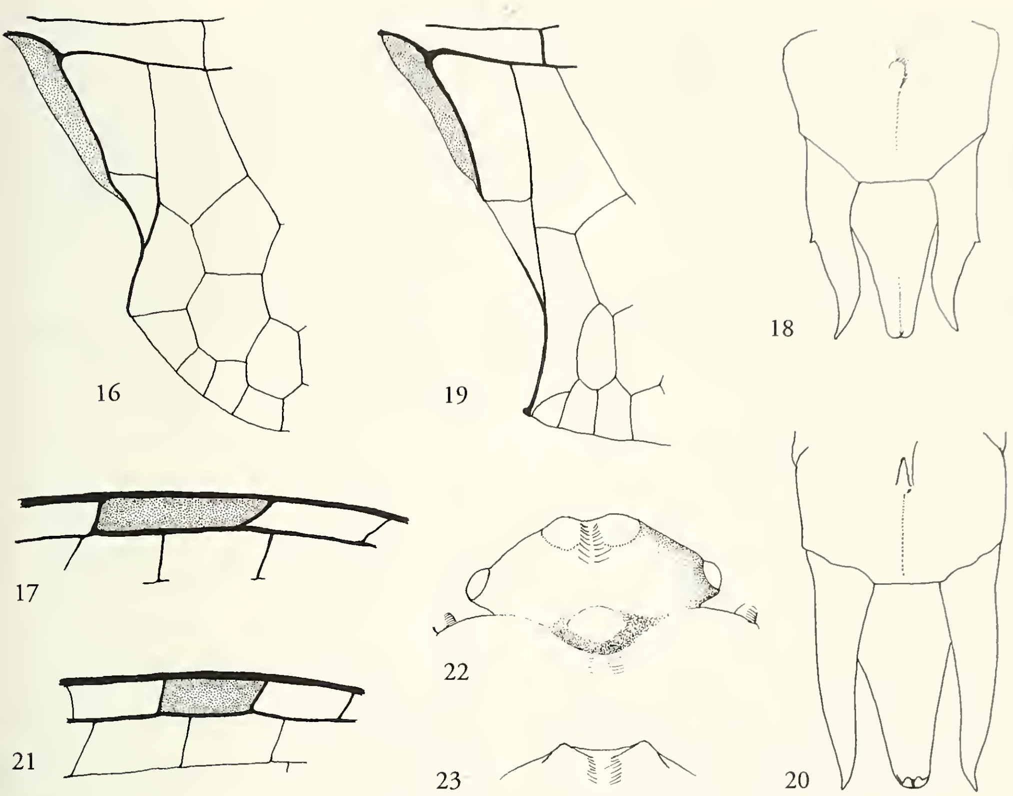
Diagnosis. – Unmistakable among Indo-Australian *Macromia*: head, thorax and abdomen brown without any metallic lustre. Structural characters: wing base with anal angle sharp, but not angulated (fig. 11); the anal triangle rather short (long in *moorei fumata*), membranula ending circa halfway between anal crossvein and base of anal triangle; pterostigma rather short (fig. 12), circa twice as long as high (more than three times in *moorei fumata*); anal appendages of male with superiors with rather smooth outer margin, without any indication of tooth (figs. 9-10) (cf. *moorei fumata* and *westwoodii*); inferior appendage approximately as long as superiors (clearly shorter in *celebica*).

Description. – Little can be added to the extensive description of the male in Lieftinck (1950). Live colour of eye dark green. Since Lieftinck did not provide any illustration, I have added here drawings of the head, wing base, anal appendages and secondary genitalia (figs. 8-14). The up to now undescribed female was collected in Southeast Sulawesi.

Female. – General coloration as the male, and structurally very similar to the male, although more robust. Head and thorax not differing from male. Wings somewhat broader, especially at base; membranula fully opaque white or only greyish in most narrow part; rusty brown base of wings more extensive than in male, in costal and subcostal area of fore and hind wing reaching to first Ax or even somewhat beyond; some less extensive rusty brown at base of medio-anal space; Arculus at Ax2 in fore wing and just beyond Ax2 in hind wing; fore wing 16-17 Ax, 9 Px, 7 Cux; hind wing 10-12 Ax, 11 Px, 5 Cux. Abdomen of the coloration ('Mikado-brown') as male; segment 1 dorsum dark brown and lateral parts brown; segment 2 brown, somewhat darker above than laterally, as the male with two narrow transverse yellow streaks, one over transverse carina halfway abdominal segment and the other pair more oblique running just before posterior margin; segment 3 anteriorly brown to transverse carina, somewhat darker above, posteriorly dark brown except for space just before segment 4; segments 4-7 similar to segment 3, but dark patch anterior to transverse carina gradually increasing in size, and posterior paler brown ring also increasing from segment 4 to 7; segment 8 brown with dorsal carina black and some darkening against dorsal carina; segment brown, dorsal carina dark; segment 10 brown; appendages middle brown, rather short, acute. Valvula vulvae short, approximately four times as wide as long, with wide triangular emargination, the tips just bifid, somewhat curved inwards (fig. 15).

Other material examined. – Sulawesi Tenggara. S of Sanggona: Gunung Watuwila. Sunggai Lalonduwasi near Centipede camp. c. 1050 m. 2-4 Nov 1989 (J. van Tol) 3♂ 1♀ (JvT 5932-5935); Sulawesi Tengah, ca. 10 km WNW Palopo near Tojambu. 800-1000 m, c. 2°56'S 120°07'E, Jul/Aug 1991 (Yohan R.), 1♀ (JvT 5936), all in RMNH. I have also studied one of the specimens collected by Askew et al. (1989): 1♂, in RSME.

Remarks. – I collected this species myself along a small, shaded stream in a steep valley in the Mengkoko mountain area. The insects appeared immediately after sunrise, and were active for approxi-



Figs. 16-23, *Macromia* species. 16-18, 22, *M. westwoodii*; 19-21, 23, *M. chalciope*. – 16, 19, Base of righr hind wing, male; 27, 21, Pterostigma of right fore wing; 18, 20, Anal appendages of male, dorsal view; 22-23, Vertex in frontal view (fig. 23 dorsal-most part only).

mately one hour. Males as well as females flew low over the water up and down the stream, more or less in a straight line. With a rather slow and small wing beat, they were not extremely fast. The specimens could be collected at a site where a big log of more than one meter diameter was laying in the stream. *Macromia* specimens crossed the log at just a few centimeters height to return immediately to the water surface. The female was caught on a dark day at 16.30 h, i.e. 1.5 hours before sunset.

Macromia moorei fumata Krüger

Macromia fumata Krüger, 1899: 333-335 (Java) [not examined].

Macromia moorei fumata. – Lieftinck 1950: 678 (key, mentioned Celebes); Lieftinck 1954: 119, 185 (references, geographical distribution); Lieftinck 1971a: 29 (geographical distribution).

Remarks. – I have been able to check the specimen (in SMFD) at which Lieftinck's notice of this taxon on Sulawesi was based. Although this specimen can be assigned to *M. moorei fumata* without doubt, I consider its occurrence on Sulawesi still doubtful. The 'Lompo Battau' labels of Fruhstorfer have on many occasions proved to be incorrect (see van Tol 1987: 163). *M. moorei fumata* is rather common on Java, where Fruhstorfer also collected during his long journey through the former Dutch Indies.

Material examined. – Lompa Battau, S. Celebes, III. 1896 (H. Fruhstorfer) '16764' (in green ink) 1♂ [label in Ris' hand] [identified by M.A. Lieftinck as *Macromia moorei fumata*, Jan. 1928].

PHYLOGENETIC RELATIONSHIPS

Introduction

The so-called Papuasian representatives of *Macromia* share at least four characters (Lieftinck 1952, 1971a), viz., an exceptionally small discoidal triangle of the hind wing, a minute pterostigma of ca. one mm, a sharply acute anal angle of the hind wing in

Table 1 Character matrix for taxa of *Macromia* of the Indo-Australian archipelago.

(1)	extero-lateral tooth superior appendage	12	(present/absent)
(2)	vertex	12	(bilobed/rounded)
(3)	hamulus	12	(shorter/longer lobus)
(4)	superior appendages	12	(normal/very slender)
(5)	pterostigma	123	(long/intermediate/ very short)
(6)	postclypeus	12	(unicolorous/yellow markings)
(7)	antehumeral stripe	12	(present/absent)
(8)	anal angle	12	(sharp/angulate)
(9)	discoidal cell	12	(wide/narrow)
(10)	general coloration	12	(green/brown)
(11)	dorsal spine abdominal segment 10	123	(slender/absent/broad)
(12)	curvature superior appendages	123	(curved inward/outward/straight)

Character	1	2	3	4	5	6	7	8	9	10	11	12
Species												
amymone	1	1	2	2	3	2	2	2	2	1	2	2
celebica	2	2	1	1	2	1	1	1	2	1	2	2
chalciope	3	1	2	2	3	1	1	2	2	1	1	3
irina	2	2	1	1	2	1	2	1	2	2	2	2
melpomene	1	1	2	2	3	1	2	2	2	1	1	3
moorei fumata	1	1	1	1	1	1	2	1	1	1	2	1
terpsichore	3	1	2	2	3	2	1	2	2	1	2	3
westwoodii	1	2	1	1	1	1	1	1	1	1	3	2

the male, and long and slender genital hamules in the male. Lieftinck (1971a: 30-32) distinguishes three groups among the Papuan *Macromia* species, viz. *M. terpsichore*, *M. melpomene*, and *M. chalciope*, with the last one consisting of one species only.

The species assigned to these groups, which the exception of *viridescens* described from Cape York (Australia), are confined to the islands of New Guinea (*astarte* Lieftinck, *celaeno* Lieftinck, *eurynome* Lieftinck, *melpomene* Ris, *terpsichore* Foerster, *viridescens* Tillyard (= *amymone* Lieftinck)), the Bismarck Archipelago (*lachesis* Lieftinck), Waigeu (*euphrosyne* Lieftinck, *sophrosyne* Lieftinck) and Misool (*hermione* Lieftinck). *M. chalciope* Lieftinck is restricted to Schouten Is, and the Moluccan islands of Halmahera and Bacan (Lieftinck 1971a). No species of *Macromia* have been mentioned from any of the other Moluccan islands up to now. According to Lieftinck (1952: 460) *M. chalciope* can be considered 'an immediate derivative of the eastern cluster', i.e. that the sister-species of *chalciope* could be discovered among the species of New Guinea and adjacent islands.

The Malay peninsula and the Greater Sunda Islands are inhabited by 15 species of *Macromia* (see Lieftinck 1971a: 29). Although Lieftinck (1929) attempted to distinguish species groups in the western Malesian species, this author (1950: 716) had to admit that the groups had an artificial character. Variation in morphology among the species of western Malesia is more prominent than that among the Papuan representatives.

Finally, the Philippine islands are inhabited by at least one endemic species, viz. *M. negrito* Needham & Gyger from Luzon. The widespread *M. cincta* is reported from Palawan (Lieftinck 1929: 92), and Tawi Tawi (Lieftinck 1974), while also *M. gerstaeckeri* may

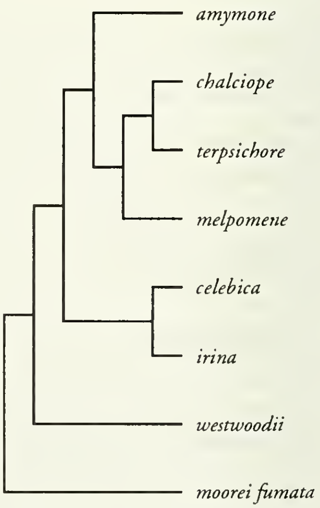


Fig. 24. Tree for *Macromia* species of the Indo-Australian archipelago.

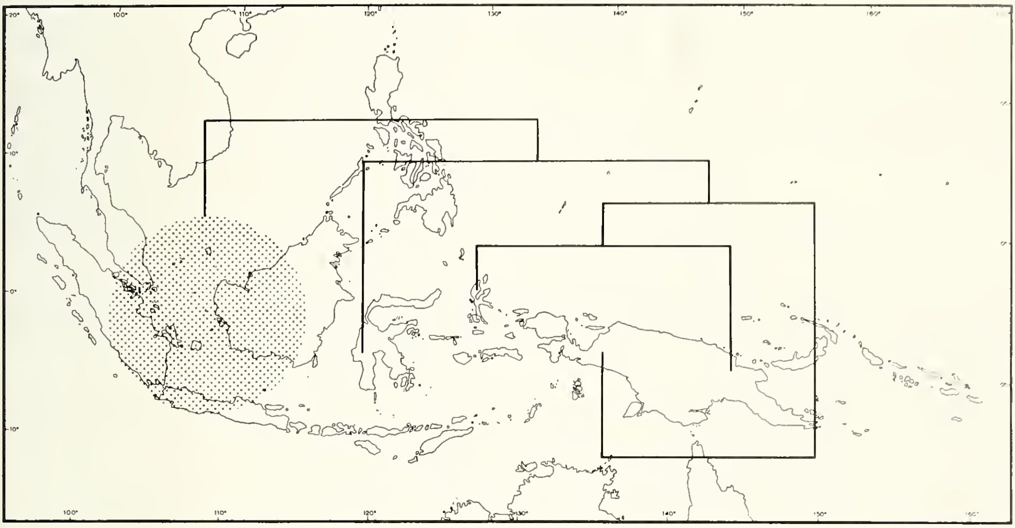


Fig. 25. Phylogenetic relationships of *Macromia* species (groups) represented on the map of Malesia.

occur in the Philippines (Lieftinck 1971a: 29).

I present here the results of a preliminary investigation of the phylogeny of the *Macromia* of the Indo-Australian region, mainly based on the characters used by Lieftinck to establish his Papuan species groups, or to distinguish the Oriental and Papuan groups. As outgroups I have added *M. moorei fumata* Krüger and *M. westwoodii* Selys, both considered closely allied to *M. irina* (Lieftinck 1950). For the present study only a limited number of the Papuan species have been included. Unfortunately, *M. negrito* Needham & Gyger from Luzon, was not available for study. A more extensive phylogenetic study, involving more of the Oriental as well as the Papuan species, has to wait for the future.

Methods and results

The matrix (table 1) was analysed with PAUP, version 3.1.1 (Swofford 1993), using 'exhaustive search'. *Macromia moorei fumata* was designated as outgroup, but the results appeared to be similar when *M. westwoodii* was selected as such. The analysis resulted in one tree of 20 steps (CI=0.800, RI=0.818).

This tree (fig. 24) shows that all Papuan species form a monophyletic group, with the Sulawesi species as sister group. The Papuan groups as defined by Lieftinck (1971a) are not corroborated by the present analysis. It is of interest to notice the sistergroup relationship of *M. terpsichore* from NE New Guinea, and *M. chalciope* from Halmahera.

Homoplasies in the present tree expecially occur in two non-structural characters, viz. character 7 (antehumeral stripe) and to a lesser extent character 6 (postclypeus).

Discussion and biogeography

The results of the phylogenetic analysis partly confirm earlier suggestions by Lieftinck on relationships among Indo-Australian *Macromia* species. Lieftinck (1950) considered *M. irina* from Sulawesi closely related to *M. moorei* and *M. westwoodii*, both rather widespread in Southeast Asia, including Borneo. The rather solid build of the superior appendage, in combination with the absence of an extero-lateral tooth, ranks the Sulawesi representatives in an intermediate position between the Oriental and the Papuan species. This intermediate position can also be recognized in the shape of the pterostigma.

The rather distant relationships of the Sulawesi and Halmahera species are of interest in a biogeographical context. Although the geological history of Wallacea and Halmahera is still under debate (e.g. Daly et al. 1991, Honza 1991), there is general agreement that there is no shared history for the North Moluccas (Halmahera) and Sulawesi. Reconstructions prior to 10-15 million years ago (Ma) are highly uncertain because of the very complicated plate movements. In the reconstruction of Daly et al. (1991) (see also Nichols & Hall 1991) Halmahera was formed at the margin of the Pacific and the Philippine plates, north of New Guinea, with a westward progression from c. 5 Ma to its present position. At least some parts of

Sulawesi have a much longer (65 million years) history above sea level on a far more western position. In other words, from approximately 60 to 5 Ma, the Oriental region + Sulawesi have shared (in some respects) a common history, while Halmahera shares its history mainly with New Guinea. The close contact of the Oriental and Papuan region is more recent than 5 Ma.

Given these phylogenetic relationships, and our present knowledge of the geological history of the area, the following historical scenario may be outlined. All *Macromia* species in the Indo-Australian region originate from an Oriental ancestor. The ancestor of the Sulawesi + Papuan species groups possibly inhabited Sulawesi, while the ancestor of the Halmahera *M. chalciope* + New Guinea *M. terpsichore* species groups apparently lived in north(eastern) New Guinea. The occurrence of two relatively remotely allied species on Sulawesi and Halmahera can be attributed to the westward movement of Halmahera during the last ten million years.

Acknowledgements

Field work in Sulawesi was supported by the Zoological Museum at Bogor. The kind help of the director of the museum, drs. Mohammad Amir, and his staff, as well as the staff of Lembaga Ilmu Pengatahuan Indonesia (Indonesian Academy of Sciences) is gratefully acknowledged. The expert knowledge of Sulawesi of Mr. Baharudin (Bantimurung) was of great help for successful collecting. Dr. H. Schröder kindly arranged the loan of material in SFMD. I also thank Dr. K. Wilson (Hongkong) for his comments on a draft of this paper.

References

Askew, R.R., G.G. Cleland, D.A.L. Davies & T.W. Harman, 1989. A report on a collection of Odonata from North Sulawesi, Indonesia. – Tijdschrift voor Entomologie 132: 115-121, fig. 1, tables 1-2.

Daly, M.C., M.A. Cooper, I. Wilson, D.G. Smith & B.G.D. Hooper, 1991. Cenozoic plate tectonics and basin evolution in Indonesia. – Marine and Petroleum Geology 8: 2-21, figs. 1-15.

Honza, E., 1991. The Tertiary arc chain in the Western Pacific. – Tectonophysics 187: 285-303, figs. 1-5.

Krüger, L., 1899. Die Odonaten von Sumatra. III. Theil. a. Familie Libelluliden (with supplement: Neue Cordulinen von Java und Borneo. – Stettiner Entomologische Zeitung 60: 321-338.

Lieftinck, M. A., 1929. A revision of the known malaysian dragonflies of the genus *Macromia* Rambur, with comparative notes on species from neighbouring countries and descriptions of new species. – Tijdschrift voor Entomologie 72: 59-108, figs. 1-22.

Lieftinck, M. A., 1950. Further studies on Southeast Asiatic species of *Macromia* Rambur, with notes on their ecology, habits and life history, and with descriptions of larvae and two new species (Odon., Epophthalmiinae). – Treubia 20: 657-716.

Lieftinck, M. A., 1952. On the Papuasian representatives of the genus *Macromia* Ramburm with descriptions of five new species and some larval forms (Odon.). – Treubia 21: 437-468, p. 1-22.

Lieftinck, M. A., 1954. Handlist of Malaysian Odonata. – Treubia 22 (Supplement): i-xiii + 1-202, map.

Lieftinck, M. A., 1971a. Studies in Oriental Corduliidae (Odonata), I. – Tijdschrift voor Entomologie 114 (1): 1-63, figs. 1-50.

Lieftinck, M. A., 1971b. A catalogue of the type-specimens of Odonata preserved in The Netherlands, with a supplementary list of the Odonata types described by Dutch scientists deposited in foreign institutional collections. – Tijdschrift voor Entomologie 114 (2): 65-139 + plate 1-7.

Lieftinck, M. A., 1974. Dragonflies collected by the Noona Dan Expedition in the southwestern Philippine Islands (Insecta, Odonata). – Steenstrupia 3: 111-147, figs. 1-26.

Nichols, G. J. & R. Hall, 1991. Basin formation and Neogene sedimentation in a backarc setting, Halmahera, eastern Indonesia. – Marin and Petroleum Geology 8 (1): 50-61, figs. 1-9.

Swofford, D. L., 1993. PAUP: Phylogenetic Analysis Using Parsimony. Version 3.1.1. – Illinois Natural History Survey, Champaign.

Tol, J. van, 1987. The Odonata of Sulawesi and adjacent islands. Part 2. The genus *Diplacina* Brauer on Sulawesi. – Zoölogische Mededelingen 61: 160-176, figs. 14-39.

Received: 2 February 1994
Accepted: 14 April 1994